

Reply

Reply to Galil, B.S.; Rinkevich, B. Comment on “Kuplik et al. *Rhopilema nomadica* in the Mediterranean: Molecular Evidence for Migration and Insights into Its Proliferation. *Diversity* 2026, 18, 94”

Zafrir Kuplik ^{1,*} , Hila Dror ^{2,3} , Karin Tamar ¹ , Alan Sutton ⁴, James Lusana ⁵ , Blandina Lugendo ⁵  and Dror L. Angel ² 

¹ The Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv 6997801, Israel; karintamar@tauex.tau.ac.il

² Recanati Institute for Maritime Studies, University of Haifa, Haifa 3498838, Israel; hilador1@tauex.tau.ac.il (H.D.); dangel@univ.haifa.ac.il (D.L.A.)

³ School of the Environment and Earth Sciences, Department of Geophysical, Atmospheric and Planetary Sciences, Tel Aviv University, Tel Aviv 6997801, Israel

⁴ Independent Researcher, Dar es Salaam 11000, Tanzania; alan@robmarine.com

⁵ Department of Aquatic Sciences and Fisheries Technology, University of Dar es Salaam, Dar es Salaam 60091, Tanzania; lusana.james@udsm.ac.tz (J.L.); blugendo@udsm.ac.tz (B.L.)

* Correspondence: zafrirkuplik@tauex.tau.ac.il

We thank Galil and Rinkevich for their interest in our recent publication [1,2]. Scientific intercourse advances understanding and we welcome the opportunity to clarify the scope and implications of our study.

Before addressing specific points, we reiterate the primary objectives of our work:

(1) To provide molecular confirmation of the presence of *Rhopilema nomadica* in the Western Indian Ocean;

(2) To explore ecological processes that may have facilitated its proliferation in the Mediterranean Sea.

Our study did not aim to resolve the fine-scale phylogeographic structure, quantify gene flow, or definitively identify a single source population. The suggestions presented in the Discussion regarding the existence of *R. nomadica* in the eastern Mediterranean were explicitly framed as hypotheses consistent with the available molecular, historical, and ecological evidence.

We also recognize that certain elements of our discussion may have been interpreted as stronger in inference than intended, and we welcome the opportunity to clarify these points.

1. Interpretation of the 1938 Haifa Photograph

Galil and Rinkevich suggest that the 1938 photograph presented in Figure 2 in our article shows a group of *Rhizostoma pulmo* rather than *R. nomadica*. The photograph is historical in nature and, as reproduced in the publication, appears at reduced resolution.

The original archival photograph is of substantially higher resolution (see Supplementary Figure S1) and allows improved visualization of morphological features (e.g., vermicular filaments), while lacking the characteristic dark violet marginal pigmentation associated with *R. pulmo*. In our assessment, these features, including the absence of violet marginal pigmentation and the presence of densely filamentous oral arms, are characteristic of *R. nomadica* and not of *R. pulmo*.



Academic Editor: Bert W. Hoeksema

Received: 17 March 2026

Revised: 3 May 2026

Accepted: 25 June 2026

Published: 16 July 2026

Copyright: © 2026 by the authors.

Licensee MDPI, Basel, Switzerland.

This article is an open access article distributed under the terms and

conditions of the [Creative Commons](https://creativecommons.org/licenses/by/4.0/)

[Attribution \(CC BY\)](https://creativecommons.org/licenses/by/4.0/) license.

We further note that, upon examination of the higher-resolution archival image, Prof. André C. Morandini also favored assignment to *Rhopilema nomadica* based on the absence of violet marginal pigmentation, the lack of terminal appendages characteristic of *Rhizostoma*, and the presence of filamentous oral arm structures.

Nevertheless, despite the higher resolution, the photograph does not provide the full suite of diagnostic taxonomic characters required for definitive species-level identification. We therefore treated this interpretation as provisional and described the species as “suggested” to be *R. nomadica*. The image was not presented as taxonomic proof and does not form a basis for any of our conclusions.

Rather, it contributes historical context to the possibility that *R. nomadica* aggregations occurred in the Levant prior to the first collected Mediterranean specimen (1976). The occurrence of *R. pulmo* swarms in the region during the 1930s does not preclude the possible co-occurrence of *R. nomadica*.

We agree that phrasing such as “could have occurred” or “might have occurred” more accurately reflects the level of uncertainty associated with this historical interpretation.

2. Red Sea Records and Species Origin

Galil and Rinkevich correctly note that *R. nomadica* was described based not only on a holotype collected off Kamaran (Yemen) in 1939, but also on additional paratype material collected in 1937–1939. We fully acknowledge this and do not question the validity or quality of the original description by Galil, Spanier and Ferguson [3], which remains foundational.

Our discussion concerns biogeographic continuity rather than taxonomic validity. While the historical specimens demonstrate that the species occurred in the Red Sea in the late 1930s, there have been no additional confirmed records from the region in the decades since, despite sustained marine research and monitoring.

We recognize that absence of recent records does not constitute definitive proof of absence. Cryptic or low-density populations may persist undetected. However, the contrast between the temporally restricted series of historical collections (1937–1939) and the well-documented, recurrent blooms in the Mediterranean remains relevant when considering potential source regions and population dynamics.

3. Adequacy of the 316 bp COI Fragment

Galil and Rinkevich argue that the 316 bp COI fragment used in our analyses is insufficient and that distinct Tanzanian haplotypes negate connectivity between Tanzanian and Mediterranean populations. This interpretation extends beyond the aims of our molecular analyses.

Our primary objective was to confirm the species identity of the Tanzanian specimens, as clearly stated in the text. For this purpose, the 316 bp COI fragment was appropriate and unambiguously recovered *R. nomadica* as a monophyletic lineage under both Maximum Likelihood and Bayesian analyses ([1], Figure 5). Interspecific divergence (16.5–18.9%) was substantially higher than intraspecific divergence ($\leq 3\%$), supporting robust taxonomic assignment.

We agree that this dataset is not sufficient to resolve population connectivity or migration pathways, and we did not intend to draw such conclusions from these data. We did not attempt to resolve the fine-scale phylogeographic structure or to identify a definitive source population. Rather, we demonstrated that *R. nomadica* occurs in the Western Indian Ocean and that these specimens are phylogenetically conspecific with Mediterranean populations.

It seems that Galil and Rinkevich devote substantial attention to works in the literature that fall outside the focus of our molecular analyses. We acknowledge that the Levantine

population genetic studies cited by Galil and Rinkevich [4,5] indeed provide detailed analyses of Mediterranean populations. However, these two papers are not directly relevant to our study, as they address questions of temporal and spatial genetic structure within the Mediterranean basin, whereas our study focuses on confirming the occurrence and phylogenetic placement of *R. nomadica* in the Western Indian Ocean. Their scope is therefore distinct from, and not comparable to, the aims of our work. As such, the two approaches are complementary but pertain to different questions about the species distribution and history. In addition, the presence of distinct COI haplotypes in Tanzania does not negate phylogenetic affinity. The discovery of additional closely related haplotypes in a previously unsampled region is consistent with a broader geographic distribution and does not contradict our molecular identification.

We recognize that prior studies on the monophyly of *Rhopilema* are indeed available in the literature; these, again, fall outside the focus of our molecular analyses. In our results we simply described the phylogenetic tree resulting from the analyses and did not intend to provide a comprehensive review of the genus-level phylogeny.

4. Levantine Population Genetic Studies

The Levantine population studies cited in the Galil and Rinkevich Comment [4,5] provide valuable insights into Mediterranean population dynamics. Our study addresses a complementary topic: the occurrence and phylogenetic placement of *R. nomadica* in the Western Indian Ocean.

By extending sampling beyond the Mediterranean, we contribute new geographic context without contradicting previous findings.

5. The Aswan High Dam Hypothesis

Our discussion of trophic and environmental changes following construction of the Aswan High Dam was presented as a mechanistic ecological hypothesis consistent with documented shifts in nutrient regimes [6], phytoplankton structure [7], and temperature [8,9], with potential cascading effects on microzooplankton dynamics [10–16].

We do not present this as a demonstrated causal linkage, but as one plausible explanation among multiple interacting drivers that may have facilitated proliferation of the medusae. We agree that alternative mechanisms, including changes in propagule pressure associated with canal modification, are equally plausible and not mutually exclusive. Understanding bloom dynamics likely requires the integration of physical, ecological, and anthropogenic factors.

6. Migration Direction

We noted in the text that anti-Lessepsian migration cannot be entirely excluded, while also indicating that an Indo-Pacific origin appears more consistent with broader biogeographic patterns. This reflects scientific caution and recognition of uncertainty rather than inconsistency.

7. Contributions of the Study

Our study provides:

- The first verified molecular confirmation of *R. nomadica* in the Western Indian Ocean, and outside the Mediterranean basin.
- The first phylogenetic integration of Indian Ocean and Mediterranean material.
- A biogeographic and ecological framework that expands discussion beyond traditional single-mechanism explanations.

By integrating molecular evidence with historical records and ecosystem-scale change, we offer a broader perspective on invasion dynamics and bloom proliferation.

8. Conclusions

Our conclusions remain carefully bounded:

- *Rhopilema nomadica* is confirmed molecularly in Tanzanian waters.
- Tanzanian and Mediterranean specimens are phylogenetically conspecific.
- The Indo-Pacific remains a plausible source region for Mediterranean populations, consistent with previous studies on Lessepsian migration and not derived solely from the present dataset.
- Ecological regime shifts may have contributed to the timing and intensity of Mediterranean proliferation, but as presented, these are hypothetical mechanisms and likely involve multiple interacting factors.

Scientific progress benefits from revisiting assumptions and integrating new data. We hope that our contribution stimulates further collaborative, multi-marker investigations across the Red Sea, Indian Ocean, and Mediterranean Sea to refine and enhance our understanding of the origin and spread of *R. nomadica*.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d18070426/s1>, Figure S1: Jellyfish in Haifa Port, 1938.

Data Availability Statement: No new data were created or analyzed in this study. Data sharing is not applicable to this article.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Kuplik, Z.; Dror, H.; Tamar, K.; Sutton, A.; Lusana, J.; Lugendo, B.; Angel, D.L. *Rhopilema nomadica* in the Mediterranean: Molecular Evidence for Migration and Insights into Its Proliferation. *Diversity* **2026**, *18*, 94. [CrossRef]
2. Galil, B.S.; Rinkevich, B. Comment on Kuplik et al. *Rhopilema nomadica* in the Mediterranean: Molecular Evidence for Migration and Insights into Its Proliferation. *Diversity* **2026**, *18*, 94. *Diversity* **2026**, *18*, 425. [CrossRef]
3. Galil, B.; Spanier, E.; Ferguson, W. The Scyphomedusae of the Mediterranean Coast of Israel, Including Two Lessepsian Migrants New to the Mediterranean. *Zool. Meded.* **1990**, *64*, 95–105.
4. Giallongo, G.; Douek, J.; Harbuzov, Z.; Galil, B.S.; Rinkevich, B. Long-Term Changes in Population Genetic Features of a Rapidly Expanding Marine Invader: Implication for Invasion Success. *Biol. Invasions* **2021**, *23*, 2541–2552. [CrossRef]
5. Douek, J.; Giallongo, G.; Harbuzov, Z.; Galil, B.S.; Rinkevich, B. Long-Term Population Genetic Features of the *Rhopilema nomadica* Jellyfish from the Israeli Mediterranean Coasts. *J. Mar. Sci. Eng.* **2024**, *12*, 171. [CrossRef]
6. Halim, Y.; Samaan, A.; Zaghloul, F.A. Estuarine Plankton of the Nile and the Effect of Freshwater. In *Fresh-Water on the Sea, Proceedings of the Influence of Fresh-Water Outflow on Biological Processes in Fjords and Coastal Waters Symposium*; The Association of Norwegian Oceanographers: Oslo, Norway, 1976.
7. Dowidar, N.M. Phytoplankton Biomass and Primary Productivity of the South-Eastern Mediterranean. *Deep Sea Res. Part A Oceanogr. Res. Pap.* **1984**, *31*, 983–1000. [CrossRef]
8. Pastor, F.; Valiente, J.A.; Khodayar, S. A Warming Mediterranean: 38 Years of Increasing Sea Surface Temperature. *Remote Sens.* **2020**, *12*, 2687. [CrossRef]
9. Dror, H.; Angel, D. Rising Seawater Temperatures Affect the Fitness of *Rhopilema nomadica* Polyps and Podocysts and the Expansion of This Medusa into the Western Mediterranean. *Mar. Ecol. Prog. Ser.* **2024**, *728*, 123–143. [CrossRef]
10. Stoecker, D.; Capuzzo, J.M. Predation on Protozoa: Its Importance to Zooplankton. *J. Plankton Res.* **1990**, *12*, 891–908. [CrossRef]
11. Jonsson, P. Particle size selection, feeding rates and growth dynamics of marine planktonic oligotrichous ciliates (Ciliophora: Oligotrichina). *Mar. Ecol. Prog. Ser.* **1986**, *33*, 265–277. [CrossRef]
12. Nixon, S.W. Replacing the Nile: Are Anthropogenic Nutrients Providing the Fertility Once Brought to the Mediterranean by a Great River? *Ambio* **2003**, *32*, 30–39. [CrossRef] [PubMed]
13. Kamiyama, T. Planktonic Ciliates as a Food Source for the Scyphozoan *Aurelia aurita* (s.l.): Feeding Activity and Assimilation of the Polyp Stage. *J. Exp. Mar. Biol. Ecol.* **2011**, *407*, 207–215. [CrossRef]

14. Kamiyama, T. Planktonic Ciliates as Food for the Scyphozoan *Aurelia aurita* (s.l.): Effects on Asexual Reproduction of the Polyp Stage. *J. Exp. Mar. Biol. Ecol.* **2013**, *445*, 21–28. [[CrossRef](#)]
15. Kamiyama, T. Planktonic Ciliates as Food for the Scyphozoan *Aurelia coerulea*: Feeding and Growth Responses of Ephyra and Metephyra Stages. *J. Oceanogr.* **2018**, *74*, 53–63.
16. Kuplik, Z.; Angel, D.L. Diet Composition and Some Observations on the Feeding Ecology of the Rhizostome *Rhopilema nomadica* in Israeli Coastal Waters. *J. Mar. Biol. Assoc. UK* **2020**, *100*, 681–689. [[CrossRef](#)]

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.